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Stability and Change of Social Relationship Quality in Captive Chimpanzees (*Pan troglodytes*)

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Abstract In social animals an individual's fitness depends partly on the quality of relationships with others. Qualitative variation in relationships has been conceptualized according to a three-dimensional structure, consisting of relationship value, compatibility, and security. However, the determinants of the components and their temporal stability are not well understood. We studied relationship quality in a newly formed group of 20 captive chimpanzees made up of several previously existing social groups. We assessed dyadic relationship quality 2 yr and again 7 yr after grouping. We confirmed the existence and stability of three relationship components and labeled them value, compatibility, and approach symmetry. Previously familiar dyads had a higher value than unfamiliar dyads, especially when they were maternally or paternally related. Compatibility was higher in dyads with only females than in dyads containing a male, but familiarity did not influence compatibility. Approach symmetry was initially higher, but later lower, in familiar than unfamiliar dyads, indicating that approach symmetry of familiar dyads decreased over time. Dyadic value and compatibility were highly stable over time, which is similar to the long relationship duration found in wild chimpanzees. In sum, relationships formed earlier in life became more valuable than those formed in later adulthood, whereas nonaggressive, compatible relationships could be formed throughout life. This suggests that for immigrating individuals, high-value relationships may be relatively difficult to establish, partly explaining why wild female chimpanzees have relatively few high-quality

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relationships with other females. Our study supports the multicomponent structure and durability of relationships in social species.

Keywords Chimpanzee · Compatibility · Relationship value · Security · Tenure

Introduction

Gregarious animals form social relationships through repeated interactions with their conspecifics. Social relationships are important because for group-living animals an individual's fitness depends not only on benefits brought about by living in a group (Kappeler and van Schaik 2002), but also on benefits obtained from specific social relationships with other individuals (Aureli and Schaffner 2002; Kummer 1978; Silk 2007). Qualitative differences among social relationships are formed by differences in the content, frequency, and pattern of interactions over time (Aureli and Schaffner 2002). Individuals derive fitness benefits from good social relationships (Schülke *et al*. 2010; Seyfarth and Cheney 2012; Silk *et al.* 2003, 2010a). Good social relationships provide partners with direct benefits such as grooming and support in aggressive conflicts, or increased tolerance near resources and, thus, decreased competition (Massen *et al*. 2010; Seyfarth and Cheney 2012; Silk 2007). Therefore, it is important to quantify the patterns and frequency of social interactions to obtain information on the characteristics that determine social relationships for an individual.

The quality of a social relationship does not vary randomly among group members. In many primates, relationships among kin are better than among nonkin because investing in a relationship with kin is beneficial via kin selection, and the common social history with kin may make them trusted allies (Seyfarth and Cheney 2012). The possibility of forming relationships with kin depends on the dispersal pattern. Typically, the same-sex kin relationships in the philopatric sex are valuable. Because female philopatry is more common in mammals than male philopatry (Greenwood 1980), female–female relationships are often the most valuable ones (Kapsalis 2004; Perry *et al*. 2008; Silk *et al*. 2010b). In species with male philopatry, (maternally) related males are preferential, high-valued partners, (e.g., chimpanzees, *Pan troglodytes*: Langergraber *et al*. 2007; Mitani 2009). However, individuals of the dispersing sex can also have good relationships with kin, especially if they immigrate to the same group ("parallel dispersal": western gorilla, *Gorilla gorilla,* females: Bradley *et al*. 2007; meta-analysis on male primates: Schoof *et al*. 2009). Moreover, unrelated individuals may form beneficial relationships with each other. Males may benefit from mixed-sex relationships by obtaining mating opportunities (Massen *et al.* 2012; Moscovice *et al*. 2010), whereas females may gain protection against males or other females (Kahlenberg *et al*. 2008), or infanticide (Palombit 2000; van Schaik and Kappeler 1997). Among unrelated same-sex individuals, beneficial relationships are often characterized by similar dominance position, because a partner's value as an alliance depends on fighting ability or dominance rank (Seyfarth 1977; *cf*. Perry *et al*. 2008). In addition, good relationships are found among individuals that have known each other for a long period, possibly because familiarity may increase predictability of partner's behavior (Massen *et al*. 2010; Silk *et al.* 2006b, 2010b). Thus, different relationship attributes, i.e., kinship,

sex combination, dominance rank, familiarity, and coresidency, may be involved in maintaining good relationships.

The quality of relationships has been described as consisting of three independent components: value, compatibility, and security (Cords and Aureli 2000). The value of a relationship concerns direct benefits, afforded by, e.g., grooming and agonistic support; compatibility describes tolerance and lack of aggression; and security consists of the consistency and predictability of behavioral interactions. This model conceptualizes various other formulations of relationship quality, based on direct fitness benefits (Kummer 1978); exchange of valuable assets, e.g., grooming (Gomes and Boesch 2011; Silk *et al*. 2010a, b); time spent in proximity (Silk *et al*. 2010a); tolerance to others' presence (Kutsukake 2003); or lack of aggression (Noë and Sluijter 1995). The three-component model has been supported in captive chimpanzees (Fraser *et al*. 2008), young ravens (*Corvus corax*: Fraser and Bugnyar 2010), and wild Japanese and Barbary macaques (*Macaca fuscata*: Majolo *et al*. 2010; *M. sylvanus*: McFarland and Majolo 2011). However, researchers found only two components, conceptually similar to value and compatibility, in spider monkeys (*Ateles geoffroyi*: Rebecchini *et al*. 2011). Thus, a multicomponent structure appears to characterize relationships, at least in large-brained vertebrates living in groups with a network of social relationships.

The determinants of good social relationships influence each of the three relationship quality components differently. Kinship increases the relationship value in many species (primates: Langergraber *et al*. 2007; Mitani 2009; Rebecchini *et al*. 2011; Seyfarth and Cheney 2012; ravens: Fraser and Bugnyar 2010). Kinship increases also the compatibility (Fraser *et al*. 2008; Majolo *et al*. 2010) and security of relationships (Fraser *et al*. 2008). Sex combination may increase value, in particular if same-sex alliances are important for an individual's fitness (Mitani 2009; Silk *et al*. 2010a) or if male–female partnerships increase mating success (Huchard *et al* 2010; Massen *et al*. 2012; Moscovice *et al* 2010). Sex combination may determine also compatibility and security (Fraser and Bugnyar 2010; Fraser *et al*. 2008; Majolo *et al*. 2010). Finally, long coresidence (also termed relationship tenure) increases relationship value and compatibility, but decreases security in captive chimpanzees (Fraser *et al*. 2008), although not in wild spider monkeys (Rebecchini *et al*. 2011).

Relationships, however, are not static because they are based on the summed social interactions between two individuals and their quality may change over time. Relationships may experience variation in quality after changes in resource availability (Henzi *et al*. 2009), or in an individual's age, sexual receptivity, resource holding potential, or ability to trade social commodities, causing variation in individual's value for others (Barrett and Henzi 2006). Yet, some relationships appear to maintain high quality for extended periods of time (Langergraber *et al*. 2009; Lehmann and Boesch 2008; Mitani 2009; Silk *et al*. 2006b, 2010b, 2012). Although kinship, sex combination, and coresidency are important determinants of relationship quality components, we know relatively little of how these factors influence long-term stability of relationship quality. Moreover, there are few studies assessing how these factors influence relationships that are formed as adults. Dispersing individuals form relationships in their new group, often at a high cost (Kahlenberg *et al*. 2008), but whether the quality of such relationships can improve over the years is unknown.

We assessed the quality of social relationships in a captive group of chimpanzees that was formed from four different groups, thus including dyads that had a different tenure of relationships (Table I). We sampled the behavior of the chimpanzees at two different time points nearly 5 yr apart. This allowed us to 1) test whether the three-component model of value, compatibility, and security describes an intrinsic structure of chimpanzee social relationships that is resilient to demographic and social changes in a group; 2) address the effects of sex combination, kinship, and long-term familiarity due to coresidency on relationship quality; and 3) assess the long-term changes in relationships that have been formed as adults. In wild chimpanzees, males form strong, cooperative, and durable bonds with each other, some of them lasting for several years. In Ngogo, Uganda, many of these high-quality relationships were between maternal or paternal brothers, but strong and durable bonds were also found between nonkin males (Langergraber *et al*. 2007; Mitani 2009). Nulliparous females typically disperse into a new community, although a few females remain in or return to their natal group to breed (Nishida *et al*. 2003; Pusey *et al*. 1997). Immigrant female chimpanzees are regularly subject to aggression from resident females (Boesch and Boesch-Achermann 2000; Nishida 1989; Pusey *et al*. 2008) and seek the proximity of males, possibly for protection (Kahlenberg *et al*. 2008). However, females can develop high-quality relationships with each other (captivity: Fraser *et al*. 2008; wild: Langergraber *et al*. 2009; Newton-Fisher 2006). Therefore, we expected to find high value and possibly high compatibility in relationships among kin, male–male dyads, female–female dyads that have coresided for a long period, and female–male dyads soon after coresidence started. We expected also to find high security among kin and long-term coresident dyads.

Methods

Subjects and Housing

We studied a group of captive chimpanzees that had been formed in September–November 2002 at the Biomedical Primate Research Centre (BPRC) in Rijswijk, The Netherlands. The group was formed from 20 individuals from four previously existing social groups (A–D, Table I). The chimpanzees had a varying rearing history: some were wild-caught (early rearing unknown), some were peer-reared, and the youngest individuals were mother-reared in a larger social group. The housing history resulted in some kin dyads (N=7) having resided in different groups as adults (groups A–D; see Table I), and potentially even having been raised in separate peer groups as juveniles. Unfortunately we could not obtain information of the early peer groups' composition. All individuals had been socially housed at all times, except possibly the wild-caught individuals prior to (or 'before') arrival at BPRC.

We conducted observation period 1 (P1) 2 yr post-introduction, in November 2004–March 2005 at the BPRC. The group included 20 individuals: 2 adult males, 1 subadult male, 13 adult females, and 4 immatures (<9 yr old, which we did not include in the data collection). In 2007, the group was relocated to the Safaripark Beekse Bergen (BB), the Netherlands. Before the move, two individuals (an adult female and her immature daughter), both from the same original group (D), had been

Table I Individuals forming the focal group: name, birth year, sex, original group membership, rearing history, kin bonds, and age in P1 and P2

Name	Birth year	Sex	Original group	Rearing history	Born; mother, sire	Age in P1	Age in P2
Hilko	1990	M	A	Peer	Captivity; Diana, Billy	15	19
Jana	1986	F	A	Peer	Captivity; Corry, Hans	19	23
Christa	1988	F	A	Peer	Captivity; Tineke, Frits	17	21
Leonne	1988	F	A	Peer	Captivity; Tasja, Frits	17	21
Nadine	1990	F	A	Peer	Captivity; Corry, Robert	15	19
Dirk	1981	M	B	Peer	Captivity; Wodka, Izaak	24	28
Gert-Jan	1995	M	B	Mother	Captivity; Centa, Dirk	10	14
Anna-Clara	1980	F	B	Peer	Captivity; Nina, Gerrit	25	29
Lenny	1982	F	B	Peer	Captivity; Indira, Gerrit	23	27
Centa	1983	F	B	Peer	Captivity; Tineke, Frits	22	26
Marieke	1997	F	B	Mother	Captivity; Lenny, Dirk	8[c]	12
Daan	1997	M	C	Mother	Captivity; Diana, Frits	8[c]	12
Ruben	1997	M	C	Mother	Captivity; Sherry, Frits	8[c]	12
Carolina	1966	F	C	Mother[b]	Wild	39	43
Diana	1967	F	C	Mother[b]	Wild	38	42
Sonja	1968	F	C	Mother[b]	Wild	37	40
Sherry	1970	F	C	Mother[b]	Wild	34	39
Joke	1996	F	C	Mother	Captivity; Carolina, Frits	9	13
Gina[a]	1968	F	D	Mother[b]	Wild	37	—
Melanie[a]	1996	F	D	Mother	Captivity; Gina, Marco	9	—

Peer-rearing involved weaning at *ca*. 1–2 yr of age (max 4 yr), after which subjects were housed together with same-aged infants.

[a] We collected data at P1 but these individuals were removed from the group before the observations of P2 at BB. Therefore, the data are not included in the study.

[b] Until capture at young age, thereafter unknown.

[c] No data collected because of subject's young age.

relocated elsewhere. The data concerning these individuals are not included in the study. We conducted observation period 2 (P2) at BB ca. 6.5 yr post-introduction in May–July 2009. The group consisted of the remaining 18 individuals: 5 adult males and 13 adult females.

At the BPRC, chimpanzees were housed in a conjoined indoor cage of two 2×5×2 m cages adjacent to smaller sleeping cages, where individuals were housed overnight in pairs or small groups. In addition, they had access to two covered outdoor compounds of 6×6 m each. The subjects were provided with enrichment objects such as ropes, tires, and cloths and fed three times per day with a mixture of commercial primate food pellets, vegetables, fruits, and seeds. Water was available *ad libitum*.

At the BB the chimpanzees had access to a grassy outdoor island of 2786 m^2 and an indoor enclosure of 173 m^2. Chimpanzees were not free to choose between indoor

and outdoor facility, but they were kept outdoors when the weather permitted it. The island contained climbing frames, platforms, and rocks, and the subjects were supplied regularly with enrichment items, e.g., ice cubes, cardboard boxes. Feeding always took place in the indoor enclosure. The chimpanzees were fed in the morning and evening in their night enclosures, which were not observable by researchers. During the daytime, chimpanzees were fed fruit or vegetables twice a day. Water was available *ad libitum*.

Data Collection and Analyses

We observed the chimpanzees all day (*ca*. 09:00 h–16:00 h; the exact times depended on the husbandry schedule) with 10-min focal animal sampling. In addition, at BB we performed short 2-min focal observations before predetermined feeding times. We obtained 168 focal observation hours (X±SD=4.9 h±0.4 per individual) in P1 and 75 focal observation hours (X±SD=5 h±0.0) per individual) in P2. Focal samples consisted of instantaneous sampling of the main activity at each minute (0.00 s) and continuous sampling of social interactions for 10 min. We recorded all approaches and social behavior within two arm lengths of the focal individual. We recorded grooming as bout duration to the nearest second. We recorded aggressive conflicts *ad libitum*. We defined a conflict as an interaction involving aggressive behavior (chase, charge, or physical aggression) by one individual and screaming or fleeing by another individual.

We quantified the social relationships of the adult and subadult dyads using seven behavioral variables (Table II). We chose behaviors as close as possible to the chimpanzee study by Fraser *et al*. (2008) at Chester Zoo. However, only six of their variables were quantifiable in our study: *proximity*, *neutral or nonaggressive approaches*, *grooming*, *aggressive conflicts*, *agonistic support*, and *counter-intervention* (Table II). We deemed consistency in affiliation unreliable here because the observation periods lasted for only *ca*. 5 and 3 mo, respectively. Instead, we scored *approach symmetry.* The remaining three variables from Fraser *et al*. (2008) study were either too rarely exhibited (successful begging; grooming symmetry because many dyads never groomed each other) or too uniform across dyads (tolerance to approaches, the great majority of which were neutral in this group) to include in the analyses.

We used only data from dyads that we had observed at both times in the analyses (N=105 dyads). For each dyad, we determined the relationship quality variables for the two time periods separately. Subsequently, for each time period separately, we analyzed the variables with a principal components analysis (PCA) with Varimax rotation and Kaiser normalization. The component extraction was based on eigenvalue >1 and scree-test. In both analyses, diagnostics indicated acceptable sampling adequacy (P1: Kaiser–Meyer–Olkin measure [KMO]=0.56; P2: KMO=0.62).

Next, we analyzed the effects of three dichotomic variables —familiarity, sex combination, and kinship— on the dyadic component scores derived from the PCA. We deemed dyads that had been housed together before 2003 familiar (N=30) and considered the rest unfamiliar (N=75). Note that familiarity categorization was based on the group composition like it was immediately before 2003. However, although we could not confirm the early peer-rearing group compositions,

Table II Variables used to measure relationship quality

Variable	Operational definition
Approach	Frequency of approaches within dyad with neutral or nonaggressive behavior (A approaches B + B approaches A)
Approach symmetry	A approaches B / (A approaches B + B approaches A)
Conflict	Frequency of conflicts in dyad (A aggression toward B + B aggression toward A)
Support	Frequency of coalitionary support in conflict (A supports B + B supports A)
Countersupport	Frequency of aggression against coalition partner's conflict opponent (A with X against C + C with X against A)
Grooming	Duration of time spent grooming with the other individual (A grooms B + B grooms A)
Proximity	Proportion of instantaneous focal samples in which the other individual was in proximity (two arm lengths)

We corrected approach, approach symmetry, grooming, and proximity by the summed dyadic observation time. We used *ad libitum* sampling for aggressive conflicts, support, and countersupport, corrected by summed group observation time.

most unfamiliar dyads are likely to have resided in different groups since early juvenility. We compared sex combination between female–female dyads (N=66) and dyads including a male, i.e., male–male and male–female dyads (N=39). We lumped male–male (N=3) and male–female (N=36) dyads owing to the low number of male–male dyads. We also analyzed the data without the possible influence of the three male–male dyads. This was done by replacing the principal component scores of these three male–male dyads by the average PC scores of the male–male dyads. By comparing the two sets of results, we could assess the impact of the three male–male dyads, which turned out to be negligible. Therefore, we present only the results of the first analysis.

We defined kin dyads (N=12) as genetic parent–offspring (N=4), maternal (N=2), or paternal half-siblings (N=6). We considered all other dyads nonkin (N=93). We considered paternal siblings as kin because it increased the small sample size of the kin category and made the analyses more conservative. If kinship *per se*, not familiarity, was to increase relationships quality, paternally and maternally related individuals should have the same relationship quality (*cf*. Mitani 2009). We also derived a score of "relationship change" for each dyad for each component by calculating the difference in scores found in P1 and P2. This indicates the change of relationship quality, so that the larger the score, the more the relationship had changed in either direction.

We analyzed whether the dyadic characteristics familiarity, sex combination, or kinship affected each of the relationship quality scores at P1 and P2 as well as their change from P1 to P2 by multiple regression matrix permutation tests (also called multiple regression quadratic assignment procedure tests [mrqAP]; Dekker *et al*. 2007). In matrix permutation tests P values are assessed by means of random permutation of rows and columns of the matrix; thus, the nonindependence among the dyadic scores stemming from the same individual, i.e., among scores in the same row and scores in the same column of the respective matrices, is respected. We

applied the double semipartialing (DSP) permutation method using t as the test statistic, which is a pivotal statistic (Dekker *et al*. 2007). This DSP multiple regression matrix permutation method is implemented in the social network analysis program *sna* written in **R** by Butts (2008, 2010). In the **R** function *netlm* the following parameters were specified: mode = "graph," diag = FALSE, nullhyp = "qapspp," test.statistic = "t-value," reps=2000, indicating that the matrices are symmetric, i.e. graphs with undirected edges; that the DSP method is used, indicated by qapspp; that t is to be used as test statistic; and that 2000 permutations are performed. Because we did the testing for three sets of dyadic scores (for P1, P2, and the difference score P1 – P2) we set α at 0.016 (= 0.05/3). All tests were two-sided; thus we present Prob(|>t|), which is the two-sided P value of obtaining the absolute observed t value or a more extreme t value under the null hypothesis. We performed all tests in R version 2.13.2.

Results

In the PCA analysis for relationship quality variables in P1, we extracted three components, which explained 68.5 % of the variance. The Varimax rotated solution of the PCA is shown in Table IIIa. The first component included salient (> ±0.4) loadings of proximity, approach, grooming, and support in conflicts. We labeled this component "value." The second component had high negative loadings of aggression and of counterintervention, and consequently we labeled it "compatibility." The third component included only approach symmetry and we labeled it accordingly.

The data from P2 mostly replicated the results of P1 (Table IIIb). We extracted three components that explained 72.5 % of the variance. The first component had high loadings of proximity, approach, grooming, and support. However, support also loaded with approach symmetry on component 3, albeit more weakly. The second component encompassed negative loadings of conflicts and countersupport. The third component had a high loading of approach symmetry and a weaker loading of support.

In P1, value was significantly affected by familiarity, relatedness, and the interaction effect between these two characteristics (Table IV and Fig. 1a). Relationship value was higher among familiar than unfamiliar, and related than unrelated individuals. This effect was especially strong when related individuals were familiar, indicated by the significant interaction effect. We found a similar pattern in P2 (Fig. 1b). In addition, in P2 the sex combination had a significant effect: dyads with males (male–male and male–female dyads) had a higher value than female–female dyads. This suggests that the pattern in the value component changed little overall. Indeed, the change of relationship value over time was not significantly affected by any of the predictors.

Compatibility was significantly affected only by sex combination in P1, so that the rate of aggression was lower in female–female dyads than in male–female or male–male dyads (Table IV and Fig. 1c, d). Again, this finding was replicated in P2. Not surprisingly, therefore, the change in compatibility over time was not predicted by sex combination, familiarity, or kinship.

Table III Rotated principal components of relationship quality in P1 (a) and P2 (b)

a. P1	Value	Compatibility	Approach symmetry
Proximity	**0.77**	–0.03	0.35
Approach	**0.79**	–0.08	0.29
Grooming	**0.72**	–0.08	–0.35
Support	**0.56**	0.22	–0.16
Conflicts	0.10	**–0.85**	–0.22
Counterintervention	–0.10	**–0.86**	0.05
Approach symmetry	0.05	0.12	**0.88**
% variation explained	30.0	23.3	15.2
Eigenvalue	2.1	1.6	1.1
b. P2			
Proximity	**0.94**	–0.11	–0.03
Approach	**0.88**	–0.20	–0.17
Grooming	**0.55**	–0.39	0.03
Support	**0.54**	0.40	**0.48**
Conflicts	0.17	**–0.80**	0.03
Counterintervention	0.12	**–0.801**	0.03
Approach symmetry	-0.15	–0.13	**0.91**
% variation explained	36.8	20.1	15.6
Eigenvalue	2.6	1.4	1.1

Correlation matrix; N=105. Sampling adequacy: P1 KMO= 0.56; P2 KMO=0.62.The loadings considered as salient (> ±0.4) are shown in **bold**.

The last component describing approach symmetry was significantly affected by familiarity in P1 (Table IV): familiar dyads had higher approach symmetry than unfamiliar ones (Fig. 1e). In P2, a similarly significant but opposite effect was found. Familiar dyads had lower approach symmetry than unfamiliar ones (Fig. 1f). Consistent with this, the change in approach symmetry was significantly affected by familiarity, indicating that in time, the symmetry of approaches decreased for familiar dyads.

Discussion

Social relationships in our captive group of chimpanzees could be characterized by three independent components, which we labeled value, compatibility, and approach symmetry. The content of the components stayed largely the same 2 and 6 yr, respectively, after formation of the social group from four earlier groups. Value was especially high for kin and for familiar dyads. Compatibility was lower in dyads containing a male than in dyads containing only females. These two components were also dyadically stable over time. The third component was also affected by familiarity, but changed over time: at first familiar individuals had a higher but later a lower approach symmetry than unfamiliar individuals.

Table IV Effects of familiarity, sex combination, kinship, and familiarity–kinship interaction on the dyadic scores for three relationship components found in two observation periods, P1 and P2, and on the changes in the component scores from P1 and P2

Relationship quality component		P1			P2			P1 – P2		
		Coefficient	*t* value	Prob(>|*t*|)	Coefficient	*t* value	Prob(>|*t*|)	Coefficient	*t* value	Prob (>|*t*|)
Value	Familiarity	1.66	6.70	< 0.0001	1.55	6.52	< 0.0001	–0.11	–0.42	0.66
	Sex combination	0.29	1.82	0.075	0.71	4.62	0.001	0.42	2.46	0.06
	Kinship	1.02	4.09	0.0001	1.29	5.39	< 0.0001	0.27	1.02	0.31
	Familiar * kin	0.84	3.38	0.0005	1.22	5.12	< 0.0001	0.38	1.44	0.16
	Multiple R^2	0.40			0.45			0.12		
	Adj. multiple R^2	0.38			0.43			0.08		
Compatibility	Familiarity	0.12	0.62	0.53	0.16	0.80	0.4	0.04	0.13	0.88
	Sex combination	–0.81	–4.23	0.008	–0.84	–4.42	0.004	–0.03	–0.14	0.90
	Kinship	0.20	0.69	0.52	–0.01	–0.05	0.96	–0.21	–0.55	0.58
	Multiple R^2	0.17			0.17			0.003		
	Adj. multiple R^2	0.14			0.15			0.00		
Approach symmetry	Familiarity	0.65	3.07	0.002	–0.63	–2.98	0.005	–1.28	–4.12	0.0001
	Sex combination	0.04	0.18	0.89	–0.11	–0.56	0.58	–0.15	–0.50	0.69
	Kinship	–0.28	–0.94	0.36	0.08	0.27	0.81	0.36	0.82	0.44
	Multiple R^2	0.09			0.08			0.15		
	Adj. multiple R^2	0.06			0.06			0.12		

Prob(|>*t*|) gives the two-sided *P* value of obtaining the absolute observed *t* value or a more extreme *t* value under the null hypothesis. These *P* values are found by means of multiple regression permutation tests on the dyadic score matrices, which respect the nonindependence among scores stemming from the same individual. Familiarity: 0 = nonfamiliar; 1 = familiar. Sex combination: 0 = female–female; 1 = male–male or male–female. Kinship: 0 = nonkin; 1 = kin.

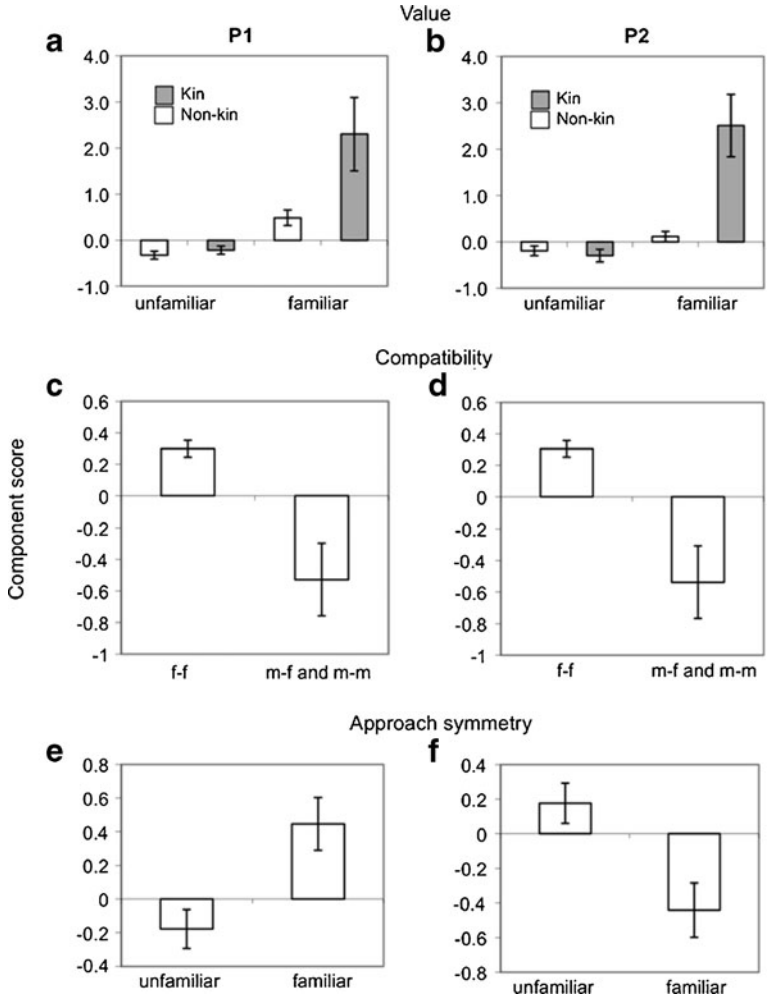

Fig. 1 Effects of dyadic relationship characteristics on relationship component scores (mean ± SE).

Three-Component Model of Relationship Quality

Similar to an early study (Fraser *et al*. 2008), we found that chimpanzee relationships consisted of three independent components. We aimed to record the same behaviors to replicate their study as closely as possible, but were unable to measure four of their variables. "Consistency in affiliation" was replaced by "approach symmetry," while the other three missing variables could not be approximated. Notwithstanding these differences, our results were very similar to those of Fraser and colleagues (2008) for two of the three components. The contents of the first component reflect direct value afforded by the relationship, as it consisted of proximity, grooming, and support. The second component contained aggression and counterintervention, and consequently was labeled compatibility. These two components were also found in ravens (Fraser and Bugnyar 2010), Japanese macaques (Majolo *et al*. 2010), Barbary macaques (McFarland and Majolo 2011), and spider monkeys (Rebecchini *et al*. 2011).

Moreover, the contents of these two components are congruent with the definitions in the literature (Cords and Aureli 2000; Kummer 1978; Massen *et al*. 2010). The third component in our study consisted of approach symmetry, which we used as a replacement of consistency of affiliation. However, symmetry in interaction at a given time describes the current state of affairs rather than the predictability of behavior in time. The importance of asymmetry in affiliative interactions has recently been highlighted as an important aspect of relationships (Majolo *et al*. 2010; McFarland and Majolo 2011). Grooming asymmetry formed an independent dyadic relationship quality component in Barbary macaques, and when interactions were analyzed individually, asymmetry in relationships was found in grooming, aggression, and agonistic support, although not in approaches (McFarland and Majolo 2011). Our results support the notion of asymmetric relationships. We also found that agonistic support loaded relatively highly (although less so than on the value component) with approach symmetry in P2, indicating that dyads with symmetric relationships supported each other in conflicts, whereas this was not found in P1. In sum, the intrinsic, multicomponent structure of relationship quality was supported in captive chimpanzees, which strengthens its significance in describing intragroup relationships among primates and possibly other social species. The generality and influence of asymmetry on the relationship quality model requires further research.

Effects of Sex, Kinship, and Familiarity on Relationship Quality Components and Their Stability

Relationship value was higher in familiar and related dyads in both study periods, and especially high for dyads that were both familiar and kin. This is consistent with the findings in captive chimpanzees (Fraser *et al*. 2008) and wild male chimpanzees, in which proximity, grooming, and support frequency is higher in maternal and paternal kin dyads (Langergraber *et al*. 2007; Mitani 2009), although kinship does not determine relationship quality in wild female chimpanzees (Langergraber *et al*. 2009). The kinship effect on relationship value is found also in other mammals, including humans (Massen *et al*. 2010; Seyfarth and Cheney 2012). Dyadic value stayed consistent long term, which is congruent with the finding that strong bonds remain stable for years in wild chimpanzees (Langergraber *et al*. 2007, 2009; Mitani 2009) and chacma and yellow baboons (Silk *et al*. 2006b, 2010a, b, 2012).

The strong positive effect of long-term familiarity on relationship value indicates that relationships formed as adults, or a relatively short time ago, were less valuable than those in which individuals had known each other for a long time. This effect persisted in time, as previously unfamiliar dyads did not increase their relationship value several years later. This suggests that truly valuable friendships in chimpanzees are less likely to be formed later in adulthood.

The interaction effect of familiarity and kinship indicated that familiar and related individuals had a higher value than familiar but unrelated ones. This suggests that familiarity and kinship had partly independent effects on relationship value. However, the peculiar rearing conditions may have contributed to this finding. Whereas some kin dyads (N=5) had been housed together in the same group, others came from different groups and thus were unfamiliar with each other (N=7). Moreover, the unfamiliar kin dyads are likely to have always been separated, because they probably grew up in

different peer groups, based on their birth years. Individuals that were reared with unrelated age-mates may not have treated their unfamiliar genetic kin differently from unfamiliar nonkin individuals, indicating that they may not recognize unfamiliar kin (*cf*. Parr and de Waal 1999). Unfortunately, we could not verify the peer-rearing group compositions to determine whether indeed unfamiliar kin dyads grew up in different peer groups and, conversely, which of the familiar dyads had been raised together as peers and which ones had been grouped together later as adults. In natural populations, such a situation is uncommon because kin are usually familiar with each other. In chimpanzees, unfamiliar related dyads are most likely to be female siblings with a large age difference, which immigrate to the same group as adults. Our results suggest that such unfamiliar but related females may nevertheless be more likely to form valuable relationships with one another than with unrelated females (*cf*. Langergraber *et al*. 2009).

We predicted that male–male and female–male dyads would have higher value than female–female dyads, but this was largely not supported. That is, male–male and male–female dyads had a higher value than female–female dyads in P2 but not in P1. Consistent with this, the direction and magnitude of dyadic relationship change revealed a marginal, though not significant, increase in the value of male–male and male–female relationships in 4 yr compared to female–female relationships. This implies that time slightly improved male relationship value, or decreased female relationship value. As we could not separate male–male and male–female relationships owing to the low number of male–male dyads, we cannot assess whether this was due to male–male or male–female relationships, or both. However, a reanalysis removing the effect of male–male dyads produced nearly identical results, indicating that the few male–male dyads had a negligible impact on the change of relationship value. Nevertheless, the small sex effect on value shows that female–female relationships in captivity can be similarly valuable to male–male relationships and also fairly stable, which corroborates earlier descriptions (de Waal 1996) and studies (Fraser *et al*. 2008).

Compatibility was lower in male–male and male–female dyads than in female–female dyads in both study periods, supporting earlier findings in chimpanzees and ravens (Fraser and Bugnyar 2010; Fraser *et al*. 2008). This indicates that dyads with males are more aggressive than female–female dyads, congruent with the more general finding that male chimpanzees are more aggressive than females (Muller 2002). Yet, there was considerable variation within the sex combinations, indicating that not only a difference between males and females, but also the identity of the dyad affects compatibility. Kinship and familiarity did not influence compatibility, contradicting our predictions. Thus, although relationships formed in adulthood may not become highly valuable, they may nevertheless be nonaggressive and tolerant. Further, some kin dyads appeared to have incompatible relationships with high rates of aggression. This finding may be driven by the related dyads that did not recognize each other as kin.

Approach symmetry was predicted by familiarity, so that in P1 familiar dyads had higher symmetry and in P2 they had lower symmetry than unfamiliar dyads. Familiar dyads thus became more asymmetric in time. This broadly agrees with the negative effect of familiarity on relationship security found in captive chimpanzees (Fraser *et al*. 2008). However, contra to our expectation, kinship and sex combination had no

effect on approach symmetry. Taken together with the results on the other components, familiar dyads appeared to have a stable value but decreasing symmetry of interactions. This presents an apparent contradiction, as we would expect the most valuable friends to also be reciprocal to maintain the balanced exchange of mutual benefits (Gilby and Wrangham 2008; Mitani 2009; Schino and Aureli 2010; Silk *et al*. 2010a). However, in the captive colony of the Yerkes Primate Research Centre, chimpanzees that had resided together for longer showed less aversion to inequity in an unequal payoff paradigm (Brosnan *et al*. 2005). This may support the idea that familiarity increases relationship asymmetry by increasing tolerance to it, and therefore reduces the damage that unbalanced exchanges may cause to a relationship (Deutsch 1975; de Waal 1997). Whether our finding is a real pattern or an artefact due to relatively small sample size should be assessed in future studies.

Implications for Welfare and Zoo Management

Our findings are relevant for captive management and welfare of chimpanzees. Adult chimpanzees, both female and male, are often transferred to other zoos, but little is known of their relationship formation in the new environments. Our results indicate that long coresidency results in higher value relationships, but that both sexes are able to form new relationships of high compatibility even in their new group. Moreover, once formed, these relationships appear to remain stable over several years. This suggests that the integration of new individuals in a group should be measured not only as a lack of aggression, but also as integration in the proximity, grooming, and support network.

Conclusions

We showed that the three-component model of relationship quality, initially studied in the Chester zoo chimpanzees, was corroborated in another group of captive chimpanzees. The model was also supported in a reassessment nearly 5 yr later, indicating that the components describe an intrinsic structure of social relationships. We also showed that the dyadic relationship quality was largely stable over several years. Relationship quality in these adult chimpanzees was influenced by the duration of their acquaintance, so that long-term familiar dyads had a higher relationship value than dyads with a shorter time of acquaintance. Although it was not possible to establish whether the familiar relationships had been formed as immatures or in adulthood, we showed that highly valuable friendships were durable and based on long-term familiarity. In contrast, compatibility was not influenced by familiarity; thus both sexes were able to form tolerant relationships as adults, independent of their prior familiarity. In natural populations, only immigrating females have to form social bonds as adults with unfamiliar individuals, whereas males can form relationships throughout development. Our results suggest that immigrant females may need a relatively long time to establish valuable relationships with resident females while compatible relationships may be faster to acquire. However, because both males and females have highly durable social relationships, but also relationships of shorter duration, both sexes show flexibility in bond formation as adults. Our results support

the general finding that primates form durable social bonds, and further illuminate chimpanzees' behavioral flexibility in social bond formation.

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